

The Soil and its Total Metabolism

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Introduction

The total amount of energy which is derived from sunlight and incorporated in plant tissues through photosynthesis varies remarkably little between terrestrial ecosystems in the same latitude. Further, since plant respiration as well as photosynthesis is increased at higher temperatures, the difference in the *net* primary production does not vary greatly with latitude.

A net dry matter production of 1 kg/m²/year (containing about 4,800 Kcal of energy) is a useful figure to remember and most normal terrestrial and fresh-water communities will neither fall short of this nor exceed it by a factor of more than two. (Some swamp systems may be up to eight times as productive however.) (Newbould, 1963), (Pearsall and Gorham, 1956).

This value of just under 5,000 Kcal is about 1.6% of the total photosynthetically useful solar energy at the earth's surface in temperate oceanic climates.

Although there is little variation in the value of net primary production, the partitioning of this energy between different parts of an ecosystem varies greatly, as does the calorific value of the living plant material which is supporting the photosynthetic activity (Table I).

It will be seen that in communities based on microscopic plants the ratio of stock to gross production is very small, and the proportion of net production consumed by herbivores is high. In woodland and forest the much larger stock of plant tissue respire more, so that proportionately less is available as secondary production. Of this again, a higher proportion is consumed by decomposer organisms. The two grassland examples show an intermediate value of stock, a low respiration value and a very high contribution to the decomposer part of the ecosystem.

It is only relatively recently that it has been realised what a high proportion of total organic matter in many terrestrial systems is present in the soil and litter and is decomposed there (Macfadyen, 1964). Clearly it is important to

TABLE I. Partition of primary production in different communities.
(Units are equivalents of kg dry matter/m²/year = 10 tonnes/Ha/year)

Community	Gross Primary production	Respiration	Net primary production			Mean Stock
			Total	Eaten	Decomposed	
Plankton: marine						
temperate	0.72	0.06	0.65	0.65	0.01	0.004
Algae: salt marsh	0.50	0.05	0.45	0.45	0.01	0.003
Spartina: salt marsh	1.17	0.10	1.07	0.07	1.00	1.06
Meadow: grazed	1.17	0.12	1.05	0.39	0.66	1.00
Beech wood: Denmark	2.35	1.00	1.35	0.95	0.40	15.5
Rain Forest: Ivory Coast	5.35	4.00	1.35	0.90	0.45	24.0

Derived percentages from above figures

Community	Gross primary production	Respiration	Net primary production			Mean stock S. prodn.
			Total	Eaten	Decomposed	
Plankton: marine						
temperate	100	9	90+	90	5	0.6
Algae: salt marsh	100	10	90+	90	5	0.6
Spartina: salt marsh	100	9	91	6	85	90
Meadow: grazed	100	10	90	33	56	85
Beech wood: Denmark	100	43	57	40	17	6,600
Rain Forest: Ivory Coast	100	75	26	17	9	4,570

Figures derived from Bray (1964), Macfadyen (1964, and in prep.), Maldaque and Hilger (1963), Muller *et al.* (1960), and Odum and Smalley (1959).

study the process of decomposition of this matter both because much of the energy originating from primary production is released there, and also because it is only during this release that plant nutrients are made available for re-cycling to the system as a whole.

The metabolic activity of soil is the sum total of that of all the constituent soil inhabiting organisms. In the case of a few desert environments direct

oxidation of soil organic matter occurs to a small extent. Also some decomposition is undoubtedly carried on by extracellular enzymes from micro-organisms, but this is presumably proportional to microbial population levels and is generally thought to be of minor importance (Hofmann, 1963).

Obviously, therefore, the greater part of total soil-metabolism could, in theory, be computed from the study of metabolism by all the organisms present. Unfortunately, although we now have reasonably accurate laboratory methods for measuring respiration of most organisms, we are a very long way from being able to relate these measurements to the environmental conditions actually obtaining in the field, to the physiological state of the organisms living there, and to the actual numbers of these organisms. In fact, the relatively fundamental question of estimating numbers of soil organisms is very far from being answered in many cases, whilst microbial metabolism in the field has not been measured directly at all.

Methods for the measurement of total soil metabolism

Most of the estimates of total soil metabolism made hitherto have been arrived at either by subtracting the energy consumed by herbivores from net primary production or by adding up estimates of the total metabolism of all the constituent organisms present. The first method is, theoretically, quite sound, but it compounds the errors from both these measurements and it is clearly desirable to attempt an independent measurement of the energy both going into the decomposer system and that leaving it. In a balanced system and in the absence of gains, losses or accumulation of organic matter in the soil these two should, of course, be equal.

The rate of addition of some components of organic matter to soil can be measured relatively easily. In woodlands, the leaf fall is measured directly: this has been done in many classical studies (e.g. Möller, Müller and Nielsen, 1954) and is a feature of current IBP programme (see Medwecka-Kornas, in prep.). However, appreciable amounts of organic matter are also added as faeces from herbivorous and carnivorous animals, and there are also gains and losses due to movements of animals between the soil and other parts of the system. In the case of grasses and many other plants the accurate measurement of litter production is far from easy, whilst the measurement of the contribution made by roots to soil organic matter is extremely difficult, and has in fact hardly been seriously attempted yet.

In order to relate litter fall to corresponding expected carbon dioxide production a conversion factor must either be determined or assumed.

Theoretically, in the case of all carbon compounds, $E_c = \frac{H}{C}$ where:—

E_c = energy content per g Carbon

H = heat of combustion per g substance in kcal

C = carbon content of substance (expressed as a decimal)

Since each 22.4 litres of CO_2 are equivalent to 12 g of Carbon, if E_{CO_2} = energy liberated in the evolution of 1 litre of CO_2 = $\frac{E_c \times 12}{22.4} \times 0.535 E_c$

$$\text{then } E_{CO_2} = \frac{0.535 H}{C}$$

For example, in the case of pinewood we have $H = 4.785$ kcal/g, $C = 0.482$ (48.2%) $\therefore E_c = 9.92$ kcal and $E_{CO_2} = 5.3$ kcal/G; corresponding figures for starch or cellulose would be $H = 3.74$, $C = 0.40$, $E_c = 9.36$ and $E_{CO_2} = 5.0$.

Quite different methods have also been used to obtain comparative data on litter decomposition and to assess the relative contributions made to the decomposition process by different groups of organisms. In particular bags of plastic fibre such as 'Nylon' and 'Terylene' containing weighed amounts of litter have been exposed in the field for controlled periods and the losses in weight or in surface area of punched litter discs have been measured and related to the litter type, mesh size of the bag and to the vegetation and environmental factors in the exposure site (Bocock and Gilbert, 1957; Bocock *et al.*, 1960; Crossley and Hoglund, 1962; Edwards and Heath, 1963; Witkamp and Olson, 1963). Although results of such methods have been shown to correlate with microbial counts and litter carbon dioxide output (Witkamp, 1966a) they cannot, of course, be used directly to give data for comparison with primary and secondary production of litter fall.

The second possibility is to attempt to add up the metabolism under field conditions of all the organisms present. Work on these lines is progressing all the time but the more we know, the greater seems to be the complexity of the task. For instance it has been shown that metabolic activity of soil arthropods depends on age, sex, reproductive condition and season (Phillipson, 1960a, 1960b, 1967; Phillipson and Watson, 1965). There is some disagreement between workers in this field as to the effect of temperature on metabolism. Some have measured Q_{10} factors as high as five or six (Berthet,

1964), others around 2 (Krogh, 1914; Nielsen and Evans, 1960; Jørgensen, 1916) and (Webb, in prep.) whilst other authors maintain that the temperature effect is insignificant (Phillipson, 1967).

The effects of other environmental variables including moisture and soil gas concentrations have hardly been measured as yet.

Further, there are whole groups of important soil organisms for which it is simply not yet practicable to assess metabolic activity, and this applies especially to the most important group of all, the micro-organisms.

Clearly, if we are not to wait for a generation or more whilst these difficulties are resolved, those of us who are interested in (a) assessing the role of soil in metabolic studies of whole ecosystems and (b) attempting to gain even a first idea of the relative importance of particular groups of soil-organisms as compared with the soil biota as a whole, must try to measure total soil metabolism.

It follows, therefore, that as at least a partial check on the technique of summing individual organisms, metabolism and the 'litter fall' method of measuring the input to the soil, it is desirable to try to measure the overall decomposition rate of organic material. The only way in which this can be done is by measuring the entire metabolic activity of the soil. In theory, of course, metabolic activity can be measured directly by calorimetry or indirectly through oxygen consumption or carbon dioxide output. At least two of these quantities are needed in order to estimate the respiratory quotient, which is likely to be abnormal especially under anaerobic conditions. In practice soil calorimetry has hardly been attempted yet (but see Lemée *et al.*, 1958).

There has been a long history of soil respirometry based on gas analysis (Macfadyen, in prep.); in most cases carbon dioxide output rather than oxygen uptake has been measured. Earlier authors (Russell and Appleyard, 1925; Waksman and Starkey, 1924) were more interested in the composition of soil atmosphere than the production of gas, and tended to use soil which had been transferred to the laboratory. They ignored the effects of disturbance and of factors such as temperature, humidity and carbon dioxide levels on soil respiration; all of these have now been shown to have considerable effects. Many workers have removed soil samples to the laboratory and, after various preparatory treatments, measured respiration in conventional respirometers (Waksman and Starkey, 1924; Gaarder, 1957) or in electrolytic respirometers (e.g. Swaby and Passey, 1953; Birch and Friend, 1956).

On the other hand authors have made field measurements by covering soil *in situ* with a bell jar or other open ended container; carbon dioxide output

is, then, measured in one of the following ways:

- (a) Estimation of increase in carbon dioxide content of the enclosed air by periodical analysis of small samples extracted at intervals (e.g. Köpf, 1952).
- (b) Continuous absorption of carbon dioxide in alkali and determination of the amount absorbed at the end of the experiment either by titration (Romell, 1927; Lundegardh, 1927; Lieth and Ouellette, 1962; Walter and Haber, 1957; Schultze, 1967) or gravimetrically (Monteith *et al.*, 1964; Howard, 1966).
- (c) Continuous circulation of air from the enclosure by means of a pump together with absorption of carbon dioxide from the gas stream in alkali. This is followed by titration or gravimetric estimation (Wallis and Wilde, 1957).

A comparison between results obtained from litter fall and from soil respiration is given in Table II. It is at once obvious that soil respiration methods produce higher estimates than do direct litter fall measurements and that only the figures due to Witkamp (1966b) and to Macfadyen (*in prep.*) appear at all reasonable. One reason for this is that soil respiration figures include carbon dioxide derived from roots which may amount to 50% of the total in woodland soils (Bray and Gorham, 1964; Macfadyen, *in prep.*). When allowance is made for root respiration, soil respiration and litter fall, figures approximate much more closely but the former are probably still high. This is probably due to stimulation of soil metabolism by the operator, a factor which has been largely eliminated by the latest improvements in technique (Macfadyen, *in prep.*; Brown and Macfadyen, 1969).

It is hardly surprising that mechanical disturbance should increase respiration in view of the well known effects of almost any kind of disturbance in promoting microbial activity (e.g. Dobbs and Hinson, 1960). It is even possible that an increased air-flow may stimulate respiratory activity to an even greater extent because the values quoted by Wallis and Wilde are almost certainly an order of magnitude too high. This may be related to the effect of carbon dioxide on microbial activity (Macfadyen, *in press*).

A major improvement in such methods is due to Witkamp (1963, 1966a, 1966b) who probably first suggested using open-ended cylinder ('inverted box method') which could be left in the soil for long periods (weeks) in order that the effects of disturbance might be reduced. These cylinders are then capped by an air-tight cover for a short while (an hour or two) during which carbon dioxide derived from the soil is absorbed in alkali and its quantity is estimated by titration.

TABLE II. Comparisons of energy and dry matter equivalents of litter as estimated by direct measurement of litter fall compared with estimates from soil respiration.

(All figures represent total quantities per square metre per annum. All conversions are based on an equivalent of 1 kg dry matter = 4,800 kcal = 700 litres of CO₂).

Type of estimate	Author	Dry matter kg	Energy kcal	Carbon dioxide litres
(a) TEMPERATE OAKWOODS				
Litter fall mor	Drift (1963)	354	1,410	248
" mull	"	332	1,320	232
" mull	Bray and Gorham (1964)	440	1,750	308
" mull	Witkamp (1966b)	538	2,150	377
Soil respiration	" "	1,110	3,030	775
"	Macfadyen (in prep.)	500	2,000	350
"	*Feher (1933)	4,430	17,700	3,100
"	*Lundegardh (1927)	11,100	44,200	7,760
"	†*Witkamp and Drift (1961)	2,310	9,250	1,620
"	*Wallis and Wilde (1957)	35,400	142,000	24,800
(b) TROPICAL FOREST				
Litter fall	Nye (1961)	1,055	4,220	740
Soil respiration	Maldague and Hilger (1963)	3,190	13,700	2,230
(c) MISCELLANEOUS TEMPERATE HABITATS:				
SOIL RESPIRATION				
(All corrected from summer readings)				
Habitat	Country	Author	Method	
*Grassland	Norway	Gaarder (1957)	Warburg 25°C	1,330 5,660 920
*Arable	England	Russell (1950)	"	673 2,890 471
* "	Germany	Köpf (1952)	Gas samples	955 4,300 700
*Beech	Denmark	Romell (1927)	Warburg	2,130- 9,150- 1,490- 3,180 13,620 2,220

* These authors quote summer-time results only. Their results are multiplied by 0.5 to obtain very approximate mean annual figures.

† Revised figures supplied by Dr Minderman from I.T.B.O.N. records.

Results

The main factors affecting the amounts of carbon dioxide absorbed in such an apparatus are likely to be:—

(1) *Respiration from plant roots*. This factor is a major unknown in such studies, and it urgently requires investigation. Although root respiration measurements from laboratory plants under comparable physical conditions would be of some value, these are hardly realistic because roots in nature are inseparable from their rhizosphere organisms and their activity must frequently be influenced by these, and by the physical factors in the field. This is clearly a type of study in which the use of radio-active isotopes is desirable, and some work of this kind has already been started. In general botanical ecologists and physiologists have done little work on roots and few reliable estimates of their importance are available.

Bray (1963) (see also Bray and Gorham, 1964) estimated that woodland root production is usually about 20% of above ground tree production (i.e. 17% of the total) whilst Minderman (1967) obtained an almost identical figure (16.4%) for *Pinus niger* var *austriaca* growing in sandy conditions. Bray, Lawrence and Pearson (1959) calculate an equivalent ratio of 30% for maize. Chew and Chew (1965) estimated a ratio of about 12% for the creosote bush in a desert scrub community, whilst Bliss's (1966) figures suggest a root production in Alpine sedge meadow approaching 50%. It seems likely that most ratios lie between 15% and 50% with woodlands towards the lower end and grassland towards the upper end. Even if the production of tree roots should lie at the lower end of this range, however, it is likely that the relatively lower activity of their roots is more than counterbalanced by the greater biomass and respiration of trees which, on an area basis, greatly exceeds those of grasses. Referring back to Table I, it will be seen that the Danish beechwood respire at a rate equivalent to about 1 kg of dry matter/m²/year, whilst the figure for decomposition is 0.4 kg; a ratio of 2.5: 1. In the grassland the equivalent ratio at 1: 5.5 is reversed.

The effect of this very different distribution of gross primary production on the expected sources of carbon dioxide emerging from the soil surface can be seen in Table III.

Although the precise figures in this table are very approximate, in the present context of assessing the utility of soil carbon dioxide measurements as a measure of decomposition activity, it is clear that figures obtained will be much more trustworthy in the case of grassland (and heath) areas than in

TABLE III. Very approximate estimation of relative importance of root respiration in total below-ground metabolism. (Units are thousands of kcal/m²/annum).

	Beech	Grass
Total plant respiration (Table I)	4.0	0.47
Per cent of above due to roots	17%	30%
Respiration due to roots	0.68	0.14
Decomposition (Table I)	1.60	2.62
Decomposition plus roots = total sub-surface metabolism	2.28	2.76
Decomposition as percentage of total sub-surface metabolism	70%	94.9%

woodlands. In the latter case up to half the carbon dioxide might originate from tree roots and the soil carbon dioxide figures would require a large subtractive correction. In other habitats this correction might be almost negligible but evidence has been obtained (Macfadyen, in prep.) that root respiration in grass and *Calluna* heath becomes proportionately more important in summer than in winter.

(2) *Transient effects* due to changes in atmospheric pressure etc. Although serious errors might be anticipated from this source, they can, in fact, be allowed for.

(3) *The metabolic activity of the soil organisms*, as modified by temperature and other physical factors. Clearly it is important to determine the effect of such modifying factors on metabolism and to correct for the conditions obtaining at the time when measurements are made. The most important of these factors are:

Temperature. Under natural conditions this follows the relation: $Q_{10}=2$.

Humidity. Reduction of metabolic activity to about 50% under very dry conditions in sandy *Calluna* heath is possible. Over most of the year this factor will not be important in Western Europe but should be investigated in other areas with more extreme climates.

Carbon dioxide. Although possibly not of general importance, a significant effect at CO₂ concentrations which do occur naturally has been found in the *Calluna* habitat mentioned above (Macfadyen, in press; Burges and Fenton, 1963).

Conclusions

Until recently the decomposer organisms in soil were largely ignored by ecologists. Most recent work demonstrates clearly the relatively great importance of these forms as regards (1) the range of organisms present, (2) the variety of biochemical changes which take place, and (3) the relative

proportion of secondary production and heterotrophic activity occurring there. It is universally agreed by soil microbiologists and even by soil zoologists that the complete and simultaneous compilation of metabolic budgets for all organisms in a given soil type over a meaningful area and time period is an exercise which will not be completed in the foreseeable future. All we can hope to do at present is to work with representative organisms over realistic ranges of conditions and try to assess their relative importance in comparison with the whole soil ecosystem. Further, we need a means to compare the decomposer systems as a whole, both with those of other soils and also with other components of the ecosystem. For the first of these purposes a comparative measure of soil metabolism is probably adequate; quite realistic comparisons have even been made using dried and re-wetted soil samples in Warburg respirometers at standard temperatures (e.g. Chase and Gray, 1953).

However, if we are to fit the activities of soil decomposers into ecosystems as a whole, we must either measure their true activity in the field or we must determine corrections from which such data can be derived.

It appears that only one method has so far been developed which shows promise of meeting the more stringent criteria. Fortunately the method, described here, is simple and can be readily replicated. It demands careful observance of some elementary precautions in its use and results still require correction for the effects of plant root respiration. These are relatively insignificant in some types of habitat, but until methods for measuring this factor have been developed, figures for soil carbon dioxide output will be subject to a subtractive correction of up to 50% from this source in some habitats.

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